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ETHOLOGY OF DEFENSE IN THE APOSEMATIC CATERPILLAR *PAPILIO MACHAON SYRIACUS* (PAPILIONIDAE)

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ABSTRACT. In this investigation I was concerned with two aspects of the defensive ensemble of *P. machaon syriacus* larvae: behaviors which protected them from impending predatory attack and population dispersion. There was a comparatively high frequency of protective behaviors. The high frequency of response may be an adaptation against predators which can not recognize the warning signals or those which have a way of overcoming the larvae's defenses. I found that this aposematic insect was not commonly in large aggregations.

Aposematic animals are those which advertise their noxious qualities as an anti-predation technique. Clearly, the predators effectively selecting these aposematic traits will necessarily be able to detect the advertisement and gain some advantage in avoiding the noxious prey. The predator learns and remembers the undesirability of the prey (Evans & Waldbauer, 1982; but see Smith, 1977). An aposematic individual may have several different objectionable qualities in its armory, each of which may be effective against a different type of predator (Edmunds, 1974).

The larvae of *Papilio machaon syriacus* Verity (Lepidoptera: Papilionidae) are brightly colored and fairly obvious at close range. *P. machaon* larvae have been shown to be objectionable to birds (Järvi et al., 1981; Wiklund & Järvi, 1982) and ants (Eisner & Meinwald, 1965). This caterpillar seemed to be a good model for investigating certain aspects of the aposematic way of life.

I (1983) had shown that aposematic adult Lepidoptera were less likely to perform escape behaviors (elicited by predator-mimicking stimuli) than were cryptic, adult Lepidoptera. In this study I wanted to determine the frequency of apparently protective behaviors when aposematic caterpillars were subjected to various predator-like stimuli and the relative rate of habituation with these stimuli. I was also interested in finding a possible distributional correlate with aposematism. Cryptic species generally must maintain low population densities to reduce the possibility of search-image formation. Conversely, aposematic animals often form large and conspicuous aggregations (Wiklund & Järvi, 1982). Some aposematic larvae are held at low population densities by cannibalism (Williams & Gilbert, 1981). Eruptions of palatable insects are famous (e.g. locusts, armyworms), on the other hand.

METHODS

I worked in old fields and along roadsides near Jounieh, Lebanon from July through September. The last rains generally occur in late May. I performed all tests from 1000–1800 h local time when the ambient temperature ranged between 30–40°C. The caterpillars fed principally on various above ground portions of *Foeniculum vulgare* Mill. (Umbelliferae).

I tapped the substrate of resting *P. machaon syriacus* larvae in order to induce a vibration (Evans, 1978) and recorded the response. I performed this test first, since I found that I often jostled the bushes before the end of the tests. Hence, I was more sure that all caterpillars had similar treatment. I then applied one of four tactile stimuli: dorsal anterior touch (a single tap on the anterior) (group 1, n = 50), anterior squeeze (simultaneous bilateral pressure at the anterior) (group 2, n = 39), dorsal posterior touch (group 3, n = 34), and posterior squeeze (group 4, n = 55). I quickly released the bilateral pressure or the tap to avoid muting any response. The duration (±0.1 s) and type of response (osmeterial extension, body flexion) were recorded. I then repeated the stimulus and recorded the response type. With dorsal anterior touch, possibly a minimal tactile stimulus, and with posterior squeeze, possibly a maximal tactile stimulus, I continued to administer the same stimulus every 10 s until the larva either dropped or ceased to respond thrice consecutively. This failure to respond three times in succession was interpreted as partial evidence of habituation.

Finally, I changed the second stimulus with a fifth and sixth group of larvae. I first administered a dorsal anterior touch and then an anterior squeeze to the fifth group (n = 34). With the sixth group (n = 37), I first applied a posterior dorsal touch then a posterior squeeze. The purpose of these last two test series was to compare the reactions to a different second stimulus.

No larva was used in more than one test series.

I analyzed the data using r × c contingency tables, Poisson analysis, and one-way analysis of variance (Snedecor & Cochran, 1980).

RESULTS

Initially, I was surprised at how frequently I discovered solitary *P. machaon syriacus* larvae (30.6% were alone). There was a significant divergence from the Poisson distribution ($P < 0.005$) with the majority of the high χ^2 value due to the solitaries. Later on, I observed adult females ovipositing single eggs ca. 1 m apart. Some large groups (ca. 60 plants) of *F. vulgare* had no larvae at all, but some isolated plants were heavily infested ($\leq$9 larvae/plant). These multiple infestations were quite obvious. The smaller larvae ($\leq$15 mm long) were usually feeding or resting on umbels where their color patterns were disruptive rather than aposematic. Larger caterpillars were rarely on umbels but usually on larger stems where they were effectively aposematic.

The caterpillars reacted to the stimuli by raising the anterior portion of the body (illustrated in Eisner & Meinwald, 1965), making a lateral thrust with the anterior portion of the body, and/or everting the osmeteria. The intensity of these activities varied: 1) In the minimal anterior raise, only the head and thoracic legs would rise away from the substrate; 2) In the maximum response, the anterior portion of the body would be so strongly flexed as to form a "U." The larva's lateral movement always included the head and thorax, but often the remainder of the anterior half of the body was also involved. The eversion of the osmeteria (usually moist) ranged from one-third to fully everted.

When the osmeteria were everted, I was able to smell nothing 44.7% of the time. When there was an odor, it was generally similar to butyric acid as noted by Eisner and Meinwald (1965). The surprise of the osmeterial extension and the odor might induce aversive behavior in a potential predator.

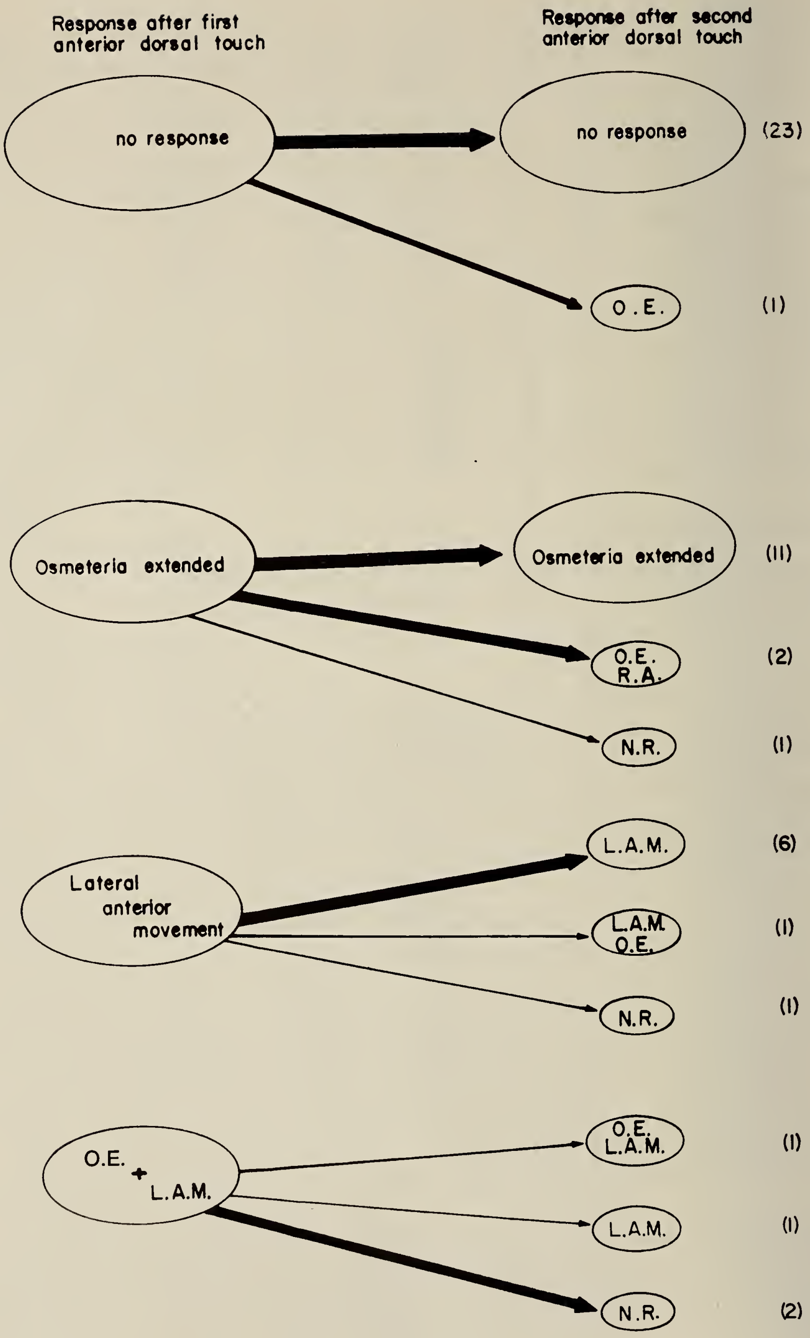
Table 1 illustrates the relative frequencies of behaviors elicited by the stimuli when administered initially. The caterpillars were significantly less likely to respond in any obvious way to substrate vibration than to the four tactile stimuli (χ^2, $P < 0.001$). The elicited responses from dorsal anterior touch were not significantly different from those with anterior squeeze (χ^2, $P > 0.10$). All other frequency comparisons were statistically significantly different (χ^2, $P \leq 0.01$). The posterior squeeze produced noticeable responses of possibly defensive value in 96% of the larvae, but substrate vibration elicited an obvious reaction in only 20%. Substrate vibration may merely indicate that a leaf gleaning bird or mammal is putting its weight on the stem (Evans, 1978). The results show that the posterior squeeze was more likely to stimulate a reaction than a dorsal posterior touch. The posterior squeeze approximates a grasp by a bird's beak and so is more similar to a real threat.

The mean durations of the various behaviors are also noted in Table 1. The means were not statistically significantly different (ANOVA, $P > 0.05$).

I wished to determine whether the larvae normally repeated the same behavior after receiving a seond similar stimulus. Fig. 1 illustrates the frequency of behaviors with the group 1 caterpillars as an example. Forty-one larvae exhibited similar behavior after the second anterior dorsal touch; only nine had different responses the second time. This

TABLE 1. Frequencies and durations of behaviors elicited by the first application of various stimuli to larvae of *Papilio machaon syriacus*. See text for a full description of behaviors and stimuli. All caterpillars were first stimulated by substrate vibration and then each was given one of the other four stimuli. Durations ±0.1 s.

	Responses						
Stimuli	No reaction	Lateral anterior movement	Lateral anterior movement + osmeterial extension	Anterior raised	Anterior raised + osmeterial extension	Osmeterial extension	Sample size
Substrate vibration	196	20	0	2	0	31	249
Dorsal anterior touch (includes group 5)	40	15	3	1	1	24	84
Anterior squeeze	14	3	6	0	0	16	39
Dorsal posterior touch (includes group 6)	24	1	2	16	27	1	71
Posterior squeeze	2	1	0	8	43	1	55
Durations ± S.D.		2.4 ± 3.83	7.8 ± 12.9	0.8 ± 0.40	6.7 ± 11.16	12.5 ± 6.54	


Response after first anterior dorsal touch
Response after second anterior dorsal touch
no response
no response
(23)
O.E.
(1)
Osmeteria extended
Osmeteria extended
(11)
O.E. R.A.
(2)
N.R.
(1)
Lateral anterior movement
L.A.M.
(6)
L.A.M. O.E.
(1)
N.R.
(1)
O.E. + L.A.M.
O.E. L.A.M.
(1)
L.A.M.
(1)
N.R.
(2)

general pattern of behavior occurred with the other three tactile stimuli when I repeated each of them. No set of second responses in any group was statistically significantly different from the set of first responses in that group (χ^2, $P \geq 0.10$).

In groups 5 and 6, I applied a different second tactile stimulus. The response frequency evoked by the anterior squeeze (as a second stimulus) was not significantly different from that appearing after the second anterior touch (χ^2, $P > 0.10$). However, the frequency was significantly different when the second stimulus was a posterior squeeze compared to when it was a repeated posterior touch (χ^2, $P < 0.05$).

In the habituation test, I found that the larvae continuing to receive the anterior dorsal touch exhibited some type of response slightly fewer times ($\bar{x} = 20.0 \pm 16.87$) than with the posterior squeeze ($\bar{x} = 20.5 \pm 13.75$). Three of the latter group eventually dropped but none of the former. The eventual failure to respond was probably not due to fatigue, since several of the non-responding larvae crawled away after I stopped applying the stimuli.

DISCUSSION

The highly localized groupings of larval *P. machaon syriacus* added to the overall impression of conspicuousness. Aposematic caterpillers often seem to feed in obvious locations (Heinrich, 1979). These larvae are distasteful to avian insectivores, and the caterpillars usually survive an attack from birds (Järvi et al., 1981; Wiklund & Järvi, 1982). The numerous aposematic larvae may act as a supernormal releaser in stimulating aversive behavior in the predator (Cott, 1940). Individual fitness may be increased in large groups of aposematic larvae since parasitoid-related mortality is reduced (Baker, 1970). Therefore, the high incidence of solitary individuals in this warningly colored species is surprising.

The degree of responsiveness to the tactile stimuli is also surprising in light of earlier work (Evans, 1983). The relatively high frequencies of responses and the reduced gregariousness could be rationalized if a large component of the mortality of the larvae were due to ants or

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FIG. 1. Frequency of reactions after a first dorsal anterior touch and then a second dorsal anterior touch. The width of the arrows is roughly proportional to the number of individuals performing the second act. **O.E.** = osmeteria extended; **R.A.** = raised anterior; **N.R.** = no observable response; **L.A.M.** = lateral anterior movement. Some activities are performed simultaneously. The parentheses at the right show the actual number performing the action. n = 50.

some other predator where learning plays a minor role in prey selection or where there would be little innate recognition of noxious prey. The most frequent responses (Table 1) included osmeterial extension as at least one component. The osmeterial secretions act primarily against ant predation (Eisner & Meinwald, 1965) but have little, if any, role in defense against bird predation (Järvi et al., 1981). Eisner and Meinwald (1965) note, however, that ants can exhaust the osmeterial secretions of these larvae by making repeated attacks. Whether or not such attacks occur in nature is unreported. The larva in such a situation might survive by throwing ants off with vigorous body thrusts.

The behavioral responses seem to be modal or fixed action patterns to the extent that they were stereotyped and appeared to have little learned component. The patterns of behavior were fixed since the same response was most often given to the same stimulus the second time. Most of the larvae eventually ceased to respond defensively. It appears that there was habituation.

CONCLUSIONS

The aposematic defensive ensemble implies a higher relative threshold for release of active protective behaviors (Evans, 1983). This principle is contingent upon a predator recognizing the aposematic signal and then avoiding contact with the noxious item. The results of this study suggest that some predators do not recognize the aposematic signal and are consistently warded off only by repeated active defenses.

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